Vol. 11: 639–655, 2019
https://doi.org/10.3354/aei00341

AQUACULTURE ENVIRONMENT INTERACTIONS
Aquacult Environ Interact

Published December 5

Dynamics and succession of plankton communities with changing nutrient levels in tropical culture ponds of whiteleg shrimp

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ABSTRACT: Optimal water quality is a prerequisite for the economic and environmental sustainability of shrimp aquaculture. The dynamics and succession of phytoplankton and microzooplankton assemblages and their interrelationship with water-quality parameters in 2 commercial ponds growing whiteleg shrimp *Litopenaeus vannamei* in south-western coastal India were assessed through periodic sampling during 96 d of culture. Of the many centric diatoms that were encountered during the initial stages of culture in nitrogen-rich conditions, only 2 dominant species, both belonging to *Thalassiosira*, persisted throughout the progression of the culture to produce a healthy bloom (up to 6×10^6 cells l^{-1}). Blooms of *Thalassiosira* spp. contributed significantly to the increased phytoplankton biomass towards the end of culture period, with a concomitant decrease in concentrations of ammonia and nitrate. The succession of pennate diatoms such as *Nitzschia closterium*, *Pleurosigma elongatum* and *Thalassionema nitzschioides* in moderate abundance was also discernible. Results of canonical correspondence analyses revealed that the progression of a diatom bloom, the emergence of dinoflagellates and the occurrence of intermittent blooms of the mixotrophic flagellate *Eutreptiella marina* were closely linked to factors such as higher temperature, salinity and phosphate concentration. Grazing by the herbivorous–bacterivorous ciliate communities may have controlled the blooms of undesirable groups of phytoplankton, ensuring better shrimp growth, higher survival and a lower food conversion ratio. Effective uptake of ammonium and nitrate by the blooming diatoms and phytoflagellates possibly prevented nutrient concentrations from reaching toxic levels, thereby generating an eco-friendly aquaculture water discharge into the adjacent ecosystem.

KEY WORDS: Diatoms · Microzooplankton · Dinoflagellate · Nutrients · Diversity · Canonical correspondence analysis · *Litopenaeus vannamei*

1. INTRODUCTION

Aquaculture of the whiteleg shrimp *Litopenaeus vannamei* (Boone, 1931) has expanded tremendously in the last decade, with a reported worldwide production of ca. 4.16 million t in 2016, which was 53% of total shrimp and prawn production (FAO 2018). Most whiteleg shrimp production is in tropical and subtropical areas of the world, mainly from Asian countries such as China, Thailand, Vietnam, Bangladesh, Indonesia and India. The obvious merits of *L. vannamei*, such as high density tolerance, adaptability to variable environmental conditions (salinity and temperature) and relatively fast growth during short culture periods (Ponce-Palafox et al. 1997, Argue et al. 2002, Roy et al. 2010), have made it the most sought-after shrimp species for commercial cultivation.

Good water quality is essential for achieving optimal shrimp growth and yield and is a prerequisite for sustainable shrimp farming. With the progression of

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culture, however, the water quality in shrimp ponds tends to deteriorate due to higher shrimp biomass and accumulation of organic matter from uneaten feed, feces and metabolites (Santhana Kumar et al. 2017, Ni et al. 2018). It has been reported that only 15% of the applied feed is transformed into shrimp biomass, whilst the remainder goes into the water and sediment (Briggs & Funge-Smith 1994). The deterioration in water quality as a consequence of nutrient build-up has been identified as a potential cause of disease outbreak in shrimp ponds (Sánchez-Martínez et al. 2007, Joshi et al. 2014)

To improve economic sustainability of shrimp culture, high-intensity grow-out systems with zero-water exchange have been developed (Boyd 1999). However, these systems generate effluents typically enriched in suspended solids, nutrients, chlorophyll *a* (chl *a*) and high biochemical oxygen demand (Páez-Osuna 2001a,b). Shrimp farm wastewater discharges in conjunction with municipal and agricultural effluents have the potential to contribute to eutrophication in the coastal environment (Burford & Williams 2001, Páez-Osuna et al. 2003, Lacerda et al. 2006, Mohanty et al. 2018). Shrimp-farming industries, therefore, are under increasing pressure to improve environmental sustainability. Since intensive shrimp aquaculture involves the input of various feeds, fertilizers and chemicals that compromise water quality, the use of bio-indicators in conjunction with physico-chemical variables to assess water quality may be beneficial.

Phytoplankton are natural biota in shrimp aquaculture ponds, and their abundance and composition are controlled by both biotic and abiotic factors. Phytoplankton are ingested by penaeid shrimps along with a variety of detrital aggregates (Dall 1968, Varadharajan & Pushparajan 2013). However, not all phytoplankton groups are desirable, as the development and blooming of harmful and toxin-producing species of cyanobacteria and dinoflagellates can negatively affect shrimp growth, survival rate and net productivity (Alonso-Rodriguez & Páez-Osuna 2003, Songsangjinda et al. 2006, Casé et al. 2008, Keawtawee et al. 2012). Diatoms are known to enhance shrimp growth, and a high proportion of diatoms in shrimp ponds is desirable (Boyd 1990). By virtue of their high nutritive value, particularly long-chain polyunsaturated fatty acids (PUFAs), many diatom species such as *Chaetoceros calcitrans*, *Skeletonema costatum*, *Thalasiossira pseudonana*, *Navicula* spp., *Nitzschia* spp. and *Amphora* spp. have long been used as live feeds in aquaculture (Brown et al. 1997, Becker 2004, Roy & Pal 2015).

Phytoplankton stabilize the whole pond ecosystem by minimizing wide fluctuations in water quality and preventing build-up of waste nutrients to toxic levels, thereby ensuring better shrimp growth and yields (Ziemann et al. 1992, Burford 1997, Lemonnier et al. 2017). A positive effect on water quality and productive shrimp performance during the co-culture of 3 species of microalgae and shrimp in a zero-water exchange system was recently demonstrated by Ge et al. (2016). Species succession is often observed in shrimp ponds, starting with some beneficial flagellate and diatom species, followed by unfavourable noxious dinoflagellates after a month of culture (Yusoff et al. 2002, Lemonnier et al. 2016, Lemonnier et al. 2017).

Phytoplankton are extensively grazed by microzooplankton (20–200 µm), which form a significant component of the natural biota of shrimp aquaculture ponds (Coman et al. 2003) and are live prey for the cultured shrimps (Calbet & Landry 2004, Cardozo et al. 2007). Therefore, microzooplankton form an important link between phytoplankton and the shrimps (Rubright et al. 1981). Studies (Tacon et al. 2002, Izquierdo et al. 2006) have shown that shrimps grow best and are healthier in aquaculture systems that have high levels of algae and other natural biota. Owing to their sensitivity to subtle changes such as low dissolved oxygen (DO) levels, high nutrient levels, toxic contaminants, poor food quality and predation occurring in the environment, both phytoplankton and microzooplankton are considered to be good bio-indicators of pond water quality and shrimp health (Casé et al. 2008, Vin 2017). In spite of key roles played by these plankton communities in regulating water quality and in shrimp diet, our knowledge on their composition, abundance, dynamics and succession in shrimp aquaculture ponds is fragmentary (e.g. Burford et al. 2003, Casé et al. 2008, Lemonnier et al. 2016). The majority of previous studies have solely characterized the phytoplankton or the environmental factors, while interrelationships — particularly with respect to water quality parameters influencing phytoplankton dynamics and succession — have received limited attention.

Against this background, the present study was undertaken to assess the abundance, composition and succession of phytoplankton and microzooplankton communities and to understand their relationship with water-quality parameters using ecological methods of classification and ordination. We aimed to demonstrate the role of abiotic factors in controlling the abundance and succession of plankton communities and the role of these communities in maintaining water quality in shrimp aquaculture ponds.

2. MATERIALS AND METHODS

2.1. Culture ponds and farm management

This study was undertaken in 2 farm ponds located near Kumta town (Karnataka state) on the south-west coast of India (14.42° N, 74.40° E). The farm is tide-fed from an adjoining creek and is located about 3 km from the coast. Two ponds (P1 and P2), having an average water depth of 1.2 m and area of ~0.84 and 1.06 ha, were chosen for the study. Management practices and inputs were similar in P1 and P2. Before stocking, the ponds were sun-dried for 1 mo and limed ($CaCO_3$) at a rate of 500 kg ha^{-1}. The ponds were then filled with dechlorinated seawater, followed by 4 ppm inorganic fertilizer (urea:single super phosphate, 1:1). Organics (wheat bran, yeast and fruit/vegetable juices) were added to enhance the growth of micro- and mesozooplankton and beneficial bacteria. Two weeks after pond preparation, stocking operations were carried out. The summer crop of 2014 with stocking in January and harvesting in April/May was considered for the study.

Healthy post-larvae (PL18) of *Litopenaeus vannamei*, produced from specific pathogen-free (SPF) broodstock and negative for white spot syndrome virus) as confirmed by PCR, were procured from a nearby commercial shrimp hatchery (Skyline Aqua Hatchery) and transported in oxygen-filled bags to the pond site. The bags were kept in pond water for about 2 h for acclimation. Actively moving PL18 with no visible signs of disease or morbidity were stocked at a density of 11 and 16 PL18 m^{-2}, respectively, in P1 and P2 during early morning hours. Lime and pH fixers were added throughout the culture period to buffer pH. The production cycle lasted 96 d of culture (DoC) with zero water exchange; the required water depth (~1 m) was maintained by adding fresh dechlorinated water on a fortnightly basis to compensate evaporation and seepage losses. Aeration was achieved using HOBAS aerators (Fernandes et al. 2010). The aeration protocol included 8 h aeration d^{-1} up to 50 DoC, 12 h d^{-1} aeration during 51–80 DoC and 16 h d^{-1} aeration thereafter until harvest.

2.2. Total food consumption, shrimp growth and survival

Shrimps were fed with commercial shrimp pellets (CP Aquaculture; proximate composition: 38–40% crude protein; 5% lipids; 3% fiber) split across 4 different feed times (06:00, 11:00, 18:00 and 23:00 h) at a rate of 10% of their body weight during the juvenile stages; feeding was gradually reduced to 2% towards the end of the culture period. Feeding rates were adjusted according to shrimp biomass and survival. The amount of feed consumed by shrimp in each meal was recorded and calculated as total food consumption per day. Food conversion ratio (FCR) was calculated at the time of harvest (96 DoC) by dividing the total feed consumed on a dry weight basis (kg) by total shrimp production in terms of wet weight (kg). Average growth of shrimp at the time of harvest was calculated by measuring the body weights of 250 shrimps.

2.3. Water sampling and analysis

Water samples for analysis of physico-chemical and biological parameters were collected 1 d prior to the transfer of PL (0 DoC) and thereafter at regular intervals (12, 24, 36, 48, 60, 72, 84 and 96 DoC) between January and April 2014 at 3 locations in the middle and edges each pond. A Niskin water sampler was used to collect pond water (30 cm above the bottom); sampling time was fixed between 09:00 and 10:00 h. Samples were kept in an icebox and transported to the laboratory for analysis.

Temperature and salinity were measured *in situ* using a thermometer and a refractometer (Atago), respectively. DO content was estimated by Winkler's method (Parsons et al. 1984). For estimation of dissolved nutrients, including ammonium (NH_4^+), nitrate (NO_3^-), nitrite (NO_2^-) and orthophosphate (PO_4^{3-}), pond water samples (250 ml) were collected in triplicate and preserved in an icebox and transported to the laboratory for analysis. In the laboratory, the water samples were filtered through cellulose filters (pore size: 0.45 µm) using a vacuum pump (Millipore) for removal of unwanted organisms or other suspended particles. Nutrient concentrations were analyzed following Parsons et al. (1984), i.e. ammonium using the salicylate method, nitrate using the cadmium reduction method, nitrite using the diazotization method and orthophosphate by the ascorbic acid method.

2.4. Plankton sampling and analysis

Plankton (phytoplankton and microzooplankton) samples were also collected at the time of water sampling. For estimation of chl *a* concentrations, 500 ml of pond water was filtered through Whatman GF/F glass fiber filter papers (47 mm diameter; nominal pore size: 0.7 µm), extracted in 90% acetone over-

night at 5°C and the fluorescence measured in a calibrated fluorometer (Turner Designs 10 AU) following Parsons et al. (1984). For estimation of plankton abundance and composition, 500 ml of pond water was filled in a clean polythene bottle and fixed with 1% Lugol's iodine and 1% formalin. The samples were allowed to settle in the dark for 48 h and then were concentrated through 20 µm mesh; aliquots were counted in Sedgewick-Rafter cells at 100–400× magnification under a calibrated inverted microscope (Olympus, BH2). Phytoplankton were identified to genus level using keys and illustrations by Subramanyan & Sarma (1961), Subramanyan (1968), Catalogue of diatoms (1985), Desikachary & Ranjithadevi (1986), Desikachary & Prema (1987), Desikachary et al. (1987) and Tomas (1997). Microzooplankton species were identified according to Hada (1938) and Jyothibabu (2004). Species richness (S) was estimated as the total number of species in a given sample. The Shannon-Weiner diversity index (H') and Pielou's evenness index (J) were used to assess plankton communities according to Shannon & Weaver (1963) and Pielou (1966), respectively.

2.5. Statistical analysis

Temporal and spatial fluctuations in water quality and plankton abundances were assessed by ANOVA (Underwood 1997) with time (DoC) and space (ponds) as sources of variation using the analysis tool pack in Microsoft Excel. Significance in all statistical tests was judged at p = 0.05. A canonical correspondence analysis (CCA) was used to evaluate the relationship between water quality parameters and groups of phytoplankton and microzooplankton using canonical community ordination (CANOCO) software for Windows v.4.5 (ter Braak & Šmilauer 2002). Abundance data were square-root transformed and a forward selection procedure of environmental variables was employed. All canonical axes were used to evaluate the significant variables under analysis at the 5% level by means of a Monte Carlo test (999 random permutations).

3. RESULTS

3.1. Water quality

ANOVA results for water quality parameters between both ponds are presented in Table 1. Except for higher concentration of DO and lower ammonia and phosphate observed in P2, most of the other parameters were similar between the ponds. Therefore, the results hereafter are combined for both ponds (mean ± SD; n = 6; Fig. 1). Water temperature was 28.0 ± 0.92°C at the beginning of culture (0 DoC), had dropped to 26.4 ± 0.07°C by 24 DoC and then increased sharply, reaching 32°C on 96 DoC ($p < 0.05$). Salinity increased significantly from 32 ± 0.71 ppt at the beginning to 44 ± 0.71 ppt at the end of the culture period. Concentrations of DO decreased from 6.8 ± 1.3 (0 DoC) to 4.4 ± 0.9 mg l^{-1} at 96 DoC, with a high value of 8.4 mg l^{-1} in the middle of the culture period. The concentrations of ammonium and nitrate, respectively, varied from 0.9 ± 0.07 to 11 ± 10 µM and from 4 ± 2.9 to 104 ± 94 µM, both decreasing towards the end of culture (96 DoC), whereas the concentration of phosphate increased from 2.7 ± 3.6 (0 DoC) to 10.4 ±12 µM towards the end of the culture period (96 DoC). The range of pH was narrow (7–8) and increased towards the end of the culture period.

3.2. Plankton biomass and abundance

Chl *a* concentration ranged from 0.6 ± 0.07 to 8.6 ± 3.5 mg m^{-3} (Fig. 2) and increased as the culture progressed. Phytoplankton cell abundance varied from 1000 ± 707 (24 DoC) to 640 131 ± 297 083 cells l^{-1} (96 Doc; Fig. 2). Microzooplankton abundance was in the range of 51 ± 14 to 145 180 ± 204 830 ind. l^{-1}; 3 uniform peaks in abundance were discernible on 24, 48 and 84–96 DoC (Fig. 2).

Table 1. ANOVA of water quality parameters between days of culture (DoC) and between the 2 ponds. DO: dissolved oxygen. *p < 0.05

Parameter	Source of variation	SS	df	MS	F	$F_{critical}$
Temp.	DoC	55.2	8	6.91	67.4*	3.44
Salinity	DoC	231	8	28.8	15.2*	3.44
DO	DoC	21	8	2.6	14.6*	3.44
Ammonia	DoC	198	8	25	1.37	3.44
Nitrate	DoC	21699	1	2712	0.09	5.32
Phosphate	DoC	177	8	22	0.98	3.44
pH	DoC	1.62	8	0.2	8.7*	3.44
Chl *a*	DoC	166	8	21	7.0*	3.44
Temp.	Pond	0.18	1	0.18	1.76	5.32
Salinity	Pond	1.4	1	1.4	0.74	5.32
DO	Pond	5.1	1	5.1	29.0*	5.32
Ammonia	Pond	14.2	1	14.2	0.79	5.32
Nitrate	Pond	193	1	193	0.12	5.32
Phosphate	Pond	208	1	208	9.22*	5.32
pH	Pond	0.08	1	0.08	3.70	5.3
Chl *a*	Pond	1.09	1	1.09	0.36	5.32

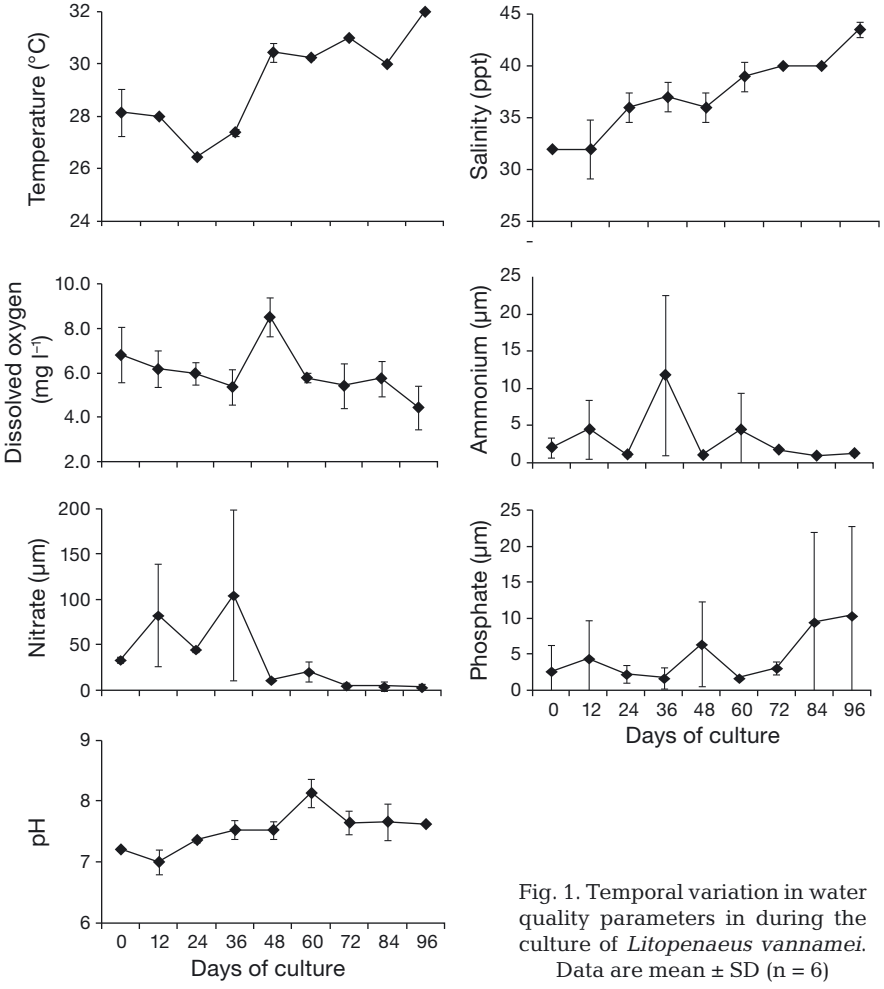

Fig. 1. Temporal variation in water quality parameters in during the culture of *Litopenaeus vannamei*. Data are mean ± SD (n = 6)

3.3. Frequency of occurrence of plankton communities

Both centric and the pennate groups of diatoms made up the phytoplankton community structure. Centric diatoms showed almost 100% frequency of occurrence (%FO) during 48–84 DoC but decreased sharply to a minimum of 22% at 96 DoC, with pennate diatoms becoming dominant (Fig. 3a). Overall, the ponds were dominated by centric diatoms. The microzooplankton comprised of ciliates, flagellates, heterotrophic dinoflagellates and larval stages of mesozooplankton (Fig. 3b). Ciliates were dominant on 0, 60 and 72 DoC, heterotrophic dinoflagellates during 12–36 DoC and flagellates on 48, 84 and 96 DoC.

3.4. Plankton community structure

In total, 59 phytoplankton species comprising mainly diatoms were recorded during the culture period (Table 2). Of these, only 16 species were centric diatoms. The major contributions to the bulk of the phytoplankton abundance throughout the culture period belonged to *Thalassiosira* spp., which progressed into a bloom >48 DoC. *Leptocylindrus minimum* attained an abundance of 3700 cells l^{-1} on 36 DoC, while the abundance of other species of centric diatoms was negligible on all DoC. Compared to the centric diatoms, more species of pennate diatoms (43) were found in the present study. They were mostly from the genera *Achnanthes*, *Navicula*, *Nitzschia* and *Pleurosigma.* Their numbers were low to moderate on most days, except on 96 DoC where a massive abundance of 165 000 cells l^{-1} of *Nitzschia closterium* was observed. *Thalassionema nitzschioides* was also found in moderate abundance (15 000 cells l^{-1}) on 36 DoC.

Microzooplankton comprised 64 species/groups (Table 3). Of these, 14 were heterotrophic dinoflagellates, the majority belonging to *Dinophysis* sp. and *Protoperidinium* sp. An unidentified dinoflagellate species with a high abundance of 75 000 cells l^{-1} contributed to the microzooplankton abundance peak on 24 DoC (Fig. 2). Although as many as 35 species of ciliates were recorded, their abundances were quite low. Moderate abundances of *Dadayiella acuta* and *Tintinnopsis acuta* were observed only on 74 DoC and *Euplotus balticus*, *E. crassus* and *Strombidium caudatum* on 96 DoC. Only 2 species of flagellates were recorded, with *Eutreptiella marina* dominating on 48 and 96 DoC (Fig. 3b) and significantly contributing to the total microzooplankton peaks on those DoC (Fig. 2). Seven mesozooplankton larval/juvenile groups comprising *Arachnactis*, decapods, naupliar and copepodite stages of copepods, trochophore of polychaetes, invertebrate eggs, foraminifera and ostracods were recorded.

3.5. Dominant species

Thalassiosira spp. were the predominant diatoms, contributing over 85% to phytoplankton abundance (Fig. 4). Of the pennate diatoms, only *N. closterium*

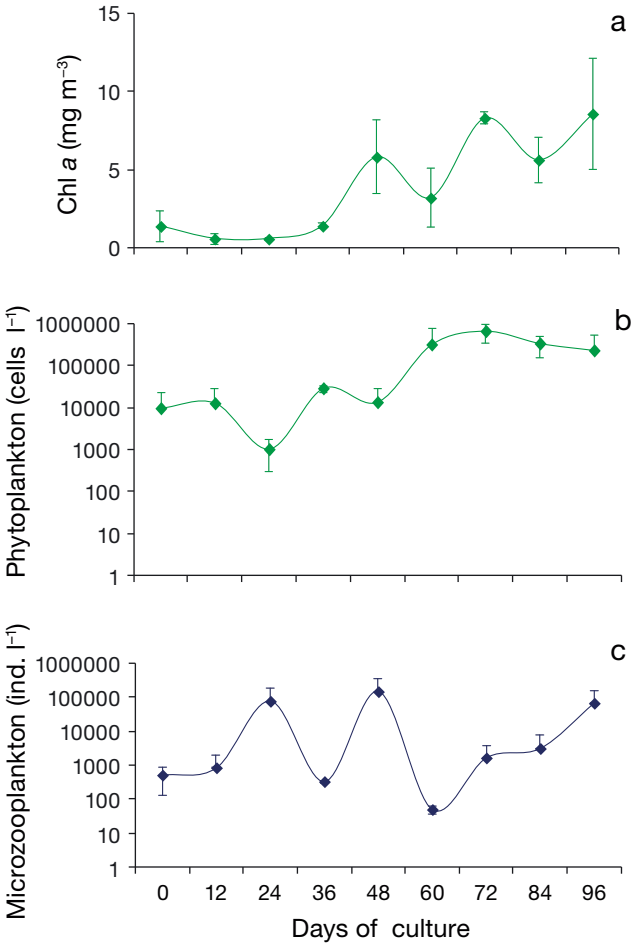

Fig. 2. Temporal variation in (a) concentration of chl *a* and abundances of (b) phytoplankton and (c) microzooplankton during the culture of *Litopenaeus vannamei.* Data are mean ± SD (n = 6)

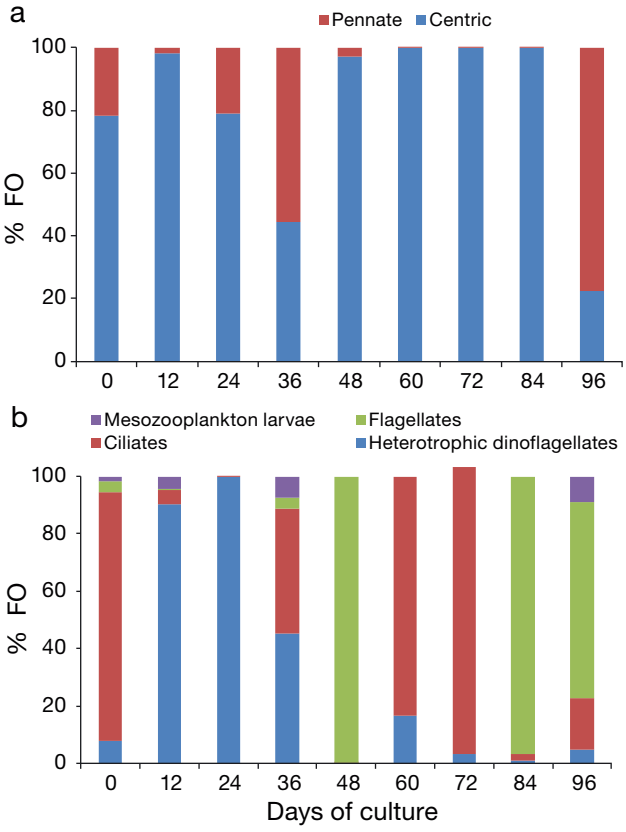

Fig. 3. Frequency of occurrence (%FO) of (a) diatom and (b) microzooplankton groups during the culture of *Litopenaeus vannamei*

contributed significantly (12.4%) and *Pleurosigma elongatum* and *T. nitzschioides* to a minor extent. Amongst the microzooplankton, the flagellate *E. marina* was the most dominant, contributing 66% to the abundance. An unidentified species of dinoflagellate (UID2) also contributed significantly (25%), while a tintinnid, *Strombidium caudatum* and the copepod nauplii and copepodites were also recorded to a minor extent.

3.6. Species diversity

The number of phytoplankton species on various DoC ranged from 6 to 32 (Fig. 5). The maximum number of species was recorded on 12 DoC and the least on 72 and 84 DoC. The diversity of phytoplankton varied from 0.01–1.58 and was higher on 24, 36 and 96 DoC. A similar trend was seen in the evenness index, which was quite low and varied from 0.003 to 0.41. The diversity indices of microzooplankton were quite similar to that of the phytoplankton. The number of species ranged from 3 to 28, with the highest value on 12 DoC and the lowest on 72 and 84 DoC. Diversity of microzooplankton varied from 0.002 to 3.0, with the higher value on 36 DoC corresponding to many species being recorded in very low abundances. Similarly, the lower diversity coincided with the occurrence of high abundance of UID2 (75 000 cells l^{-1}) on 24 DoC and 145 000 ind. l^{-1} of *E. marina* on 48 DoC (Table 3). Evenness ranged from 0.01 to 0.89, with higher values on 36, 60 and 72 DoC.

3.7. CCA

The effect of water quality on the phytoplankton and microzooplankton communities in P1 and P2 is shown in Fig. 6. Forward selection of water quality parameters retained all the 7–8 variables that significantly explained the species distribution (Table 4).

Table 2. Temporal variation in abundance (cells l^{-1}) of phytoplankton communities during the culture of *Litopenaeus vannamei* in south-western coastal India. –: not present

Code	Species	Days of culture								
		0	12	24	36	48	60	72	84	96
	Centric diatoms									
DC1	*Arcocellulus cornucervis*	–	–	2	–	–	–	–	–	–
DC2	*Cerataulina pelagica*	67	4	–	33	–	–	–	–	–
DC3	*Corethron criophilum*	–	4	–	–	–	–	–	–	–
DC4	*Cyclotella ocula*	–	–	–	13	–	–	–	–	–
DC5	*Cymatocira belgica*	–	–	2	–	–	–	–	–	–
DC6	*Dactyliosolen fragilissimus*	–	4	–	13	–	–	–	–	–
DC7	*Eucampia groenlandica*	–	4	–	–	–	–	–	–	–
DC8	*Eucampia zoodiacus*	–	4	–	–	–	–	–	–	–
DC9	*Guinardia delicatula*	–	8	–	–	–	–	–	–	–
DC10	*Guinardia striata*	–	2	–	–	–	–	–	–	–
DC11	*Leptocylindrus danicus*	–	7	–	–	–	–	–	–	–
DC12	*Leptocylindrus minimum*	–	7	3	3700	–	–	–	–	–
DC13	*Odontella longicornis*	–	4	–	–	–	–	–	–	–
DC14	*Rhizosolenia hyalina*	–	4	–	–	–	–	–	–	–
DC15	*Thalassiosira* sp.	7300	12064	202	8673	1057	307565	125000	76	50010
DC16	*Thalassiosira* sp. 1	–	–	–	–	11667	–	515000	100250	–
	Pennate diatoms									
DP17	*Achnanthes delicatula*	–	–	–	–	–	–	50	–	–
DP18	*Achnanthes exigua*	–	0.2	–	–	–	–	–	–	–
DP19	*Achnanthes frigidus*	–	–	–	33	10	–	–	–	–
DP20	*Achnanthes longipes*	–	49	–	–	–	–	–	–	–
DP21	*Amphora* sp.	–	–	–	–	–	–	50	–	–
DP22	*Amphiprora alata*	–	4	–	–	–	–	–	–	–
DP23	*Amphiprora paludosa*	–	–	–	33	–	–	–	–	–
DP24	*Cylindrotheca closterium*	–	–	–	–	–	–	–	–	360
DP25	*Cymbella marina*	–	–	–	–	–	–	–	–	–
DP26	*Diploneis suborbicularis*	–	7	–	25	20	–	–	–	–
DP27	*Epithemia adnata*	–	–	–	–	120	–	–	–	–
DP28	*Fragilaria ulna*	–	–	–	–	–	–	–	–	15
DP29	*Haslea trompii*	–	2	–	–	–	–	–	–	30
DP30	*Licmophora abbreviata*	–	–	–	–	–	–	–	–	1530
DP31	*Licmophora flabellata*	–	2	0.3	–	–	–	–	–	–
DP32	*Navicla subminiscula*	8	–	–	–	–	–	–	–	–
DP33	*Navicla transitrans*	–	–	–	–	–	20	–	25	–
DP34	*Navicula* sp.	0.4	–	2	–	–	5	–	–	60
DP35	*Navicula* sp.1	–	2	–	–	–	–	–	–	–
DP36	*Nitzschia closterium*	4	–	–	12	–	–	–	–	165000
DP37	*Nitzschia dissipata*	–	13	–	–	–	–	–	–	–
DP38	*Nitzschia longissima*	–	–	2	–	–	30	–	–	–
DP39	*Nitzschia sicula*	8	–	–	45	–	–	–	–	1500
DP40	*Nitzschia sigma*	–	7	–	–	4	35	–	–	1500
DP41	*Nitzschia* sp.	–	4	–	–	–	–	–	–	–
DP42	*Phaeodactylum tricornutum*	–	–	–	–	–	5	–	–	–
DP43	*Plagiotropis gausii*	–	–	–	–	–	–	–	–	30
DP44	*Pleurosigma angulatum*	–	7	–	–	–	–	–	–	–
DP45	*Pleurosigma capense*	8	18	–	–	26	–	–	–	–
DP46	*Pleurosigma elongatum*	1967	9	50	386	85	75	1	101	2325
DP47	*Pleurosigma directum*	–	52	–	25	30	5	–	–	–
DP48	*Pleurosigma normanii*	8	–	–	–	–	–	–	–	–
DP49	*Pleurosigma* sp.	8	8	–	–	–	–	–	–	–
DP50	*Pleurosigma* sp.1	25	8	–	–	–	–	–	–	–
DP51	*Pleurosigma* sp.2	–	2	–	–	–	–	–	75	–
DP52	*Pseudonitzschia delicatissima*	–	–	0.3	–	–	–	–	–	–
DP53	*Rhopalodia gibberula*	–	–	2	–	–	–	–	–	–
DP54	*Stauroneis constricta*	–	4	–	–	–	–	–	–	–
DP55	*Synedra formosa*	–	–	–	–	–	–	–	–	15
DP56	*Synedra ulna*	–	9	–	–	60	5	–	–	30
DP57	*Thalassionema nitzschioides*	–	–	–	15000	–	–	30	–	–
DP58	*Toxarium undulatum*	–	–	–	–	10	–	–	–	–
DP59	Unidentified species	–	–	–	13	–	–	–	–	–
Total	Centric diatoms	7367	12112	209	12431	12723	307565	640000	100326	50010
	Pennate diatoms	2038	204	56	15572	375	180	131	201	172395

Table 3. Temporal variation in abundance (ind. l^{-1}) of microzooplankton communities during the culture of *Litopenaeus vannamei* in south-western coastal India. –: not present

Code	Species	Days of culture								
		0	12	24	36	48	60	72	84	96
	Heterotrophic dinoflagellates									
Hd1	*Ceratium dens*	0.2	4	–	–	–	–	–	–	–
Hd2	*Dinophysis acuminata*	–	–	–	–	–	–	–	–	1500
Hd3	*Dinophysis acuta*	40	–	–	–	–	–	–	–	1500
Hd4	*Dinophysis* sp.	–	–	–	25	–	–	–	–	–
Hd5	*Ornithocercus steinii*	–	–	0.3	100	–	–	–	–	–
Hd6	*Protoperidinium brevipes*	–	733	–	–	–	–	–	–	15
Hd7	*Protoperidinium conicoides*	–	–	–	–	–	–	–	–	60
Hd8	*Protoperidinium conicum*	–	20	–	–	–	–	–	–	–
Hd9	*Protoperidinium pellucidum*	–	–	–	–	–	–	–	25	–
Hd10	*Prorocentrum minimum*	–	–	2	–	–	–	–	–	–
Hd11	*Pyrocystis lunula*	–	–	2	–	2	10	–	–	–
Hd12	*Zygabikodinium lenticulatum*	–	–	–	–	8	–	–	–	–
Hd13	Unidentified dinoflagellate1	–	3	–	25	–	–	–	–	–
Hd14	Unidentified dinoflagellate2	–	–	75000	–	–	–	–	–	–
Hd15	Dinoflagellate cysts	–	–	–	–	–	–	50	–	–
	Ciliates									
C16	*Acineta* sp.	–	–	–	13	–	–	–	–	–
C17	*Acanthostomella norveigica*	–	–	–	13	–	–	–	–	–
C18	*Actinosphaerium* sp.	–	4	–	–	150	–	–	–	–
C19	*Amphorides minor*	–	0.3	–	–	–	–	–	–	–
C20	*Dadayiella acuta*	–	–	–	–	–	–	1000	–	–
C21	*Epiplocycloides reticulata*	–	4	–	–	–	–	–	–	–
C22	*Euplotes balticus*	–	–	–	–	–	–	–	–	1500
C23	*Euplotes crassus*	–	–	–	–	–	–	–	–	1500
C24	*Eschaneustyla* sp.	–	4	–	–	–	5	–	–	–
C25	*Eutintinnus elongatus*	120	0.3	–	–	–	–	–	–	15
C26	*Favella ehrenbergii*	–	2	–	–	–	–	–	–	–
C27	*Favella turaikaensis*	20	–	–	–	–	–	–	–	–
C28	*Favella* sp.	20	–	–	–	–	–	–	–	–
C29	*Keronopsis* sp.	–	–	–	–	–	30	–	–	–
C30	*Laboea strobila*	280	–	–	13	–	–	–	–	–
C31	*Myrionecta rubra*	–	4	–	25	10	–	–	–	–
C32	*Rhabdonella poculum*	–	2	–	–	–	–	–	–	–
C33	*Rhabdonella amor*	–	2	–	–	–	–	–	–	–
C34	*Rhabdonella spiralis*	–	0.3	3	–	–	–	–	–	–
C35	*Salpingacantha ampla*	–	2	–	–	–	–	–	–	–
C36	*Salpingella decurtata*	–	8	–	–	–	–	–	–	–
C37	*Spirostomum* sp.	–	–	–	33	–	–	–	–	–
C38	*Strombidium conicum*	–	0.01	–	–	–	–	–	–	–
C39	*Strombilidium strobilus*	0.2	–	–	–	–	–	–	–	–
C40	*Strombilidium reticulatum*	4	–	–	–	–	–	–	–	–
C41	*Strombilidium turicum*	–	–	–	–	–	–	–	–	–
C42	*Salpingacantha* sp.	–	7	–	–	–	–	–	75	–
C43	*Strombidium caudatum*	–	–	–	15	–	–	–	–	9000
C44	*Strombidium cornucopiae*	–	–	–	–	–	5	–	–	–
C45	*Tintinnopsis entzil*	–	–	–	–	–	10	–	–	–
C46	*Tinntinnopsis aperta*	–	2	–	–	–	–	–	–	–
C47	*Tinntinnopsis fusus*	–	–	–	33	–	–	–	–	–
C48	*Tinntinnopsis minuta*	–	–	–	–	–	–	500	–	–
C49	*Trichocerca rousseleti*	–	4	–	–	–	–	–	–	–
C50	Unidentified	–	–	–	–	–	–	90	–	–
	Flagellates									
F51	*Campanoeca dilatata*	–	2	–	–	–	–	–	–	–
F52	*Eutreptiella marina*	20	–	–	13	145000	–	–	3000	45150

Table 3 (continued)

Code	Species	Days of culture								
		0	12	24	36	48	60	72	84	96
	Mesozooplankton larvae									
M53	*Arachnachtis* larvae	–	3.5	–	–	–	–	–	–	–
M54	Decapod larva	0.2	–	–	–	–	–	–	–	–
M55	Foraminifera	0.2	–	–	–	–	–	–	–	–
M56	Invertebrate egg	1.2	–	–	–	–	–	–	–	–
M57	Nauplii and copepodites	4.8	27.8	–	11.7	–	–	–	–	6000
M58	Ostracod	–	–	–	12.5	–	–	–	–	–
M59	Polychaete trocophore	2.0	6.7	–	–	–	–	–	–	–
Total	Dinoflagellates	40	760	75004	150	10	10	50	25	3075
	Ciliates	444	43	3	144	160	50	1590	75	12016
	Flagellates	20	2	0	13	145000	0	0	3000	45150
	Mesozooplankton larvae	8	38	0	24	0	0	0	0	6000

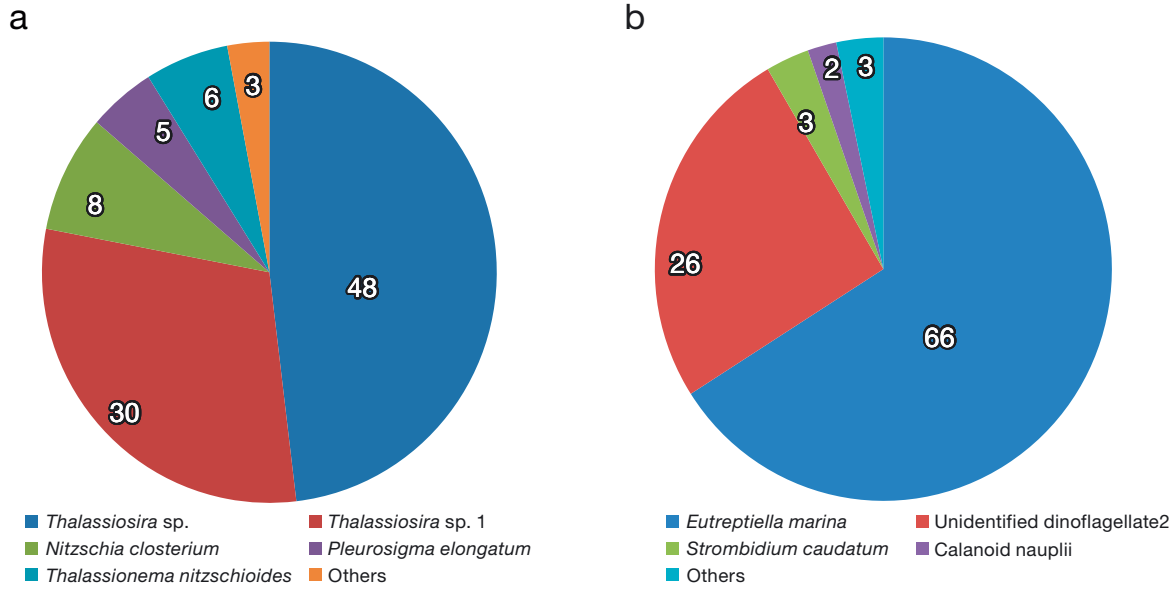

Fig. 4. Relative percent contribution of (a) phytoplankton and (b) microzooplankton species during the culture of *Litopenaeus vannamei*

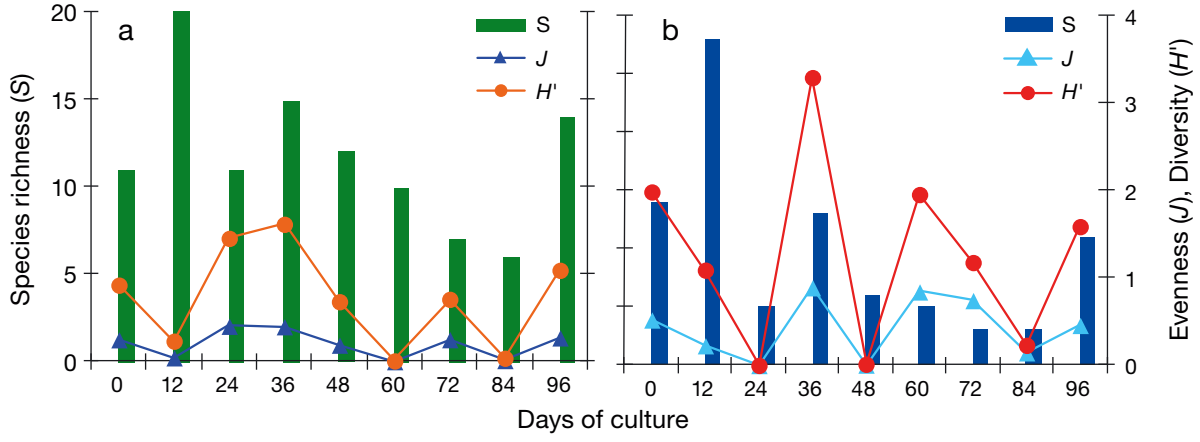

Fig. 5. Temporal variation in species diversity indices of (a) phytoplankton and (b) microzooplankton during the culture of *Litopenaeus vannamei*

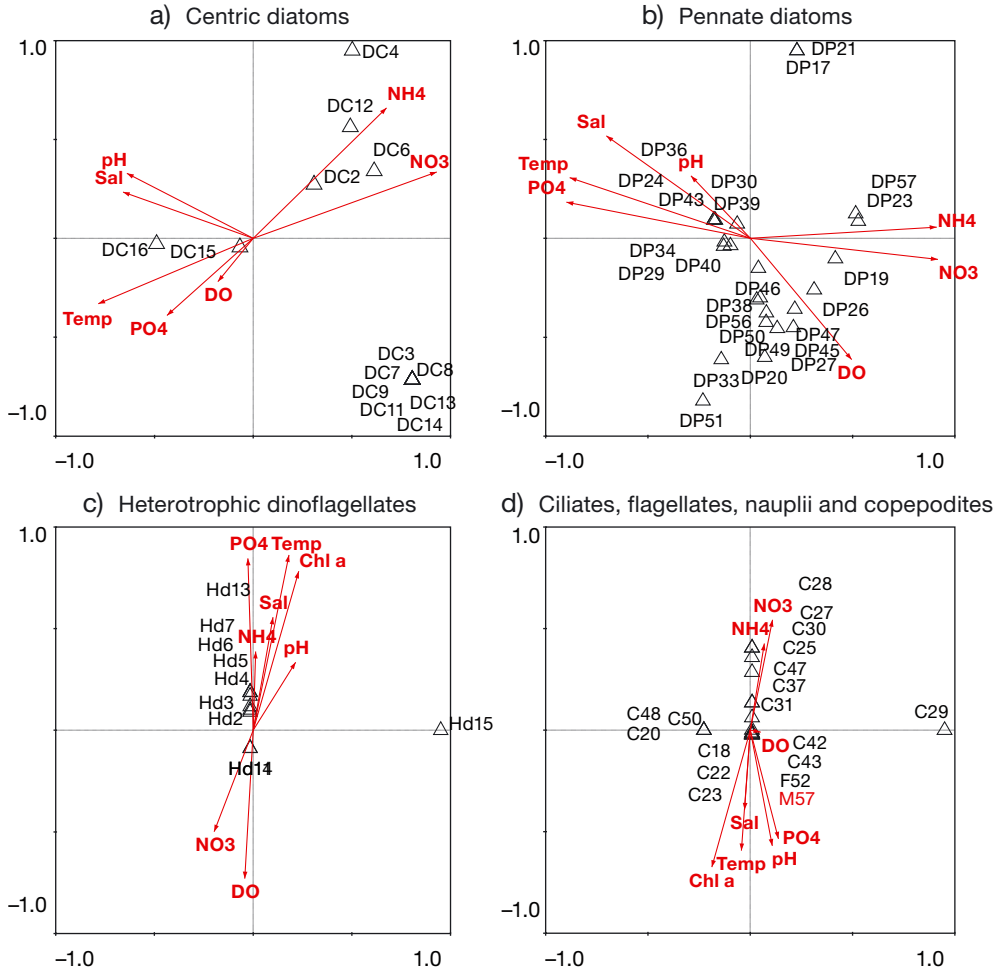

Fig. 6. Canonical correspondence analysis ordination diagram of water quality parameters with species/genus/groups of (a,b) phytoplankton and (c,d) microzooplankton during the culture of *Litopenaeus vannamei*. Results are for axis 1 (horizontal) and axis 2 (vertical); arrows represent forward-selected water quality variables (Temp: temperature; Sal: salinity; NH_4: ammonium; NO_3: nitrate; PO_4, phosphate; Chl *a*: chlorophyll *a*; DO: dissolved oxygen). Arrow length indicates the strength of that variable in explaining the species distribution during the culture; arrow direction: approximate correlation to the ordination axes. For groups/species codes, refer to Tables 2 & 3

Table 4. Summary for the 2 axes (Ax1 and Ax2) of canonical correspondence analysis with 8 selected environmental factors. % var sp-env: cumulative percentage variance of species–environment relation; eigenvalues: sum of eigenvalues and canonical eigenvalues; Cil-fla-na-co: ciliates, flagellates, nauplii and copepodites

Variable	Centric diatoms		Pennate diatoms		Dinoflagellates		Cil-fla-na-co	
	Ax1	Ax2	Ax1	Ax2	Ax1	Ax2	Ax1	Ax2
Temperature	–0.77	–0.33	–0.88	0.31	0.18	0.86	–0.04	–0.59
Salinity	–0.65	0.23	–0.70	0.52	0.10	0.56	–0.03	–0.39
Dissolved oxygen	0.18	–0.22	0.49	–0.61	–0.04	–0.73	0.05	–0.01
Ammonium	0.66	0.65	0.90	0.06	0.01	0.39	0.07	0.43
Nitrate	0.91	0.33	0.91	–0.11	–0.20	0.50	0.11	0.54
Phosphate	–0.43	–0.38	–0.89	0.18	–0.03	0.85	0.14	–0.53
pH	–0.63	0.32	–0.29	0.32	0.21	0.30	0.10	–0.57
Chl *a*					0.23	0.78	–0.18	–0.67
Eigenvalues	0.57	0.34	0.77	0.65	1.00	0.99	1.00	–0.72
% var sp-env	51.3	82.5	27.2	50.1	22.0	43.8	26.7	46.0
Total inertia		1.34		3.34		4.56		3.74
Sum eigenvalues		1.34		3.34		4.56		3.74
Sum canonical eigenvalues		1.10		2.85		4.56		3.74

In the biplot for centric diatom species (Fig. 6a), the first 2 axes (Ax1 and Ax2) explained 83% of the total variance of species–environmental data. Ax1 and Ax2 respectively explained 51 and 31% of the total variance. All canonical axes were significant ($p < 0.05$). Ax1 separated species found in a higher nitrate and ammonium environment from species corresponding to periods of higher temperature, salinity and pH. Following Ax1, the species *Ceratualina pelagica*, *Cyclotella ocular*, *Dactyliosolen fragilissimus* and *L. minimum* were found in high nitrate and ammonium conditions, whereas the increase in abundances of *Thalassiosira* spp. correlated with elevated temperature, salinity and pH.

In the biplot for pennate diatoms (Fig. 6b), Ax1 and Ax2 explained 50% of the total variance. Ax1 positively correlated with ammonium and nitrate, and the species placed along this axis were *Achnanthes frigidus*, *Amphiprora paludosa*, *Diploneis suborbicularis* and *T. nitzschioides*. The same axis negatively correlated with phosphate, temperature and salinity, and the species *Cylindrotheca closterium*, *Haslea trompii*, *Licmophora abbreviata*, *Navicula* sp., *N. closterium*, *Nitzschia sicula*, *Plagiotropis gausii* and *Nitzschia sigma* were associated with it. Along the negative side of Ax2 was the factor DO, which showed good correlation with *Epithemia adnata, Navicula transitrans*, *Nitzschia longissima*, *Pleurosigma capense*, *P. elongatum*, *P. directum*, *Pleurosigma* spp. and *Synedra ulna*.

In the biplot for dinoflagellates (Fig. 6c), Ax1 and Ax2 explained 44% of the total variance. Most of the dinoflagellates were loaded along Ax2 at higher temperature and salinity and higher concentrations of phosphate and chl *a*. On the other side of the same axis were DO and nitrate, which correlated with most dinoflagellates except an unidentified species.

In the biplot for ciliates, flagellates and copepod nauplii and copepodites (Fig. 6d), Ax1 and Ax2 explained 46% of the total variance. Most of the species were separated along Ax2. Along the positive side of this axis, species such as *Eutintinnus elongatus*, *Favella turaikaensis*, *Favella* sp., *Laboea strobila*, *Myrionecta rubra*, *Spirostomum* sp. and *Tinntinnopsis fusus* correlated with nitrate and ammonium. Along the center of Ax2 were the species *Actinosphaerium* sp., *E. balticus*, *E. crassus*, *Eutreptiella marina*, *Salpingacantha* sp., *Strombidium caudatum* and copepod nauplii and copepodites, indicating that they were influenced by factors on both sides of the axis including nitrate, ammonium, temperature, pH, chl *a* and phosphate.

3.8. Growth, survival and production of shrimp

Mean ± SE shrimp production after 96 DoC was 0.23 ± 0.07 kg m^{-2} and the final weight gain was 20.6 ± 0.3 g $shrimp^{-1}$. The survival rate was 83 ± 6.4% and the FCR was 1.56 ± 0.14.

4. DISCUSSION

In spite of differences in stocking densities between P1 and P2, the variations in major water quality parameters were similar in both ponds during the shrimp growth cycle. This may, primarily, be attributable to the common source of the inlet water and, secondarily, by good pond management practices. Being at the base of the food chain, autotrophic phytoplankton serve as a direct food source for the PL of penaeid shrimps (Coutteau 1996). Diatoms contain an average of 32–38% crude protein (Gordon et al. 2006), which is the major component of the natural food of penaeid shrimps. By contributing to DO, uptake of nutrients and supporting zooplankton grazers, phytoplankton play a pivotal role in maintaining water quality, which is critical for sustainable shrimp production (Mohanty et al. 2018). Phytoplankton abundance varied widely, from 10 to 10^5 cells l^{-1}, increasing significantly towards the end of the culture period. Among the many factors that affect phytoplankton growth and abundance, light intensity, nutrients and zooplankton grazing are important (Chien 1992). Solar irradiance is not a limiting factor in the present study, as the ponds are situated in a tropical marine region.

The influence of water temperature on the survival, growth, oxygen solubility and consumption and immune response of cultured shrimp has been documented (Guan et al. 2003, Abdelrahman et al. 2019). The initial temperature and salinity in the ponds are dependent on the inlet water and changes are driven by climatic conditions (Welch 1952). During the summer production cycle of shrimp, with stocking in January and the harvest in April, a seasonal warming along with the progress of the culture was observed. The temperature range (26–32°C) recorded during the present study has been reported to be optimal for the growth of *Litopenaeus vannamei* (Nuñez-Pastén 1988). The increase in salinity towards the end of the culture period was related to increased evaporation during the warmer months. In general, shrimps are euryhaline species and *L. vannamei* can easily adapt to varying levels of salinity (Ponce-Palafox et al. 1997).

Diatoms emerged as the major group in both ponds during 96 DoC. This is primarily because of their presence in the source water taken from the estuarine region off the west coast of India which is rich in diatoms (Pednekar et al. 2014). The high nitrate concentration, which ranged from 4–105 µM in the ponds, is favorable for the growth of diatoms (Malone 1980). The dominance of particular algal groups in aquaculture ponds is affected by abiotic and biotic factors such as salinity (Chien 1992), light (Burford 1997), pond-flushing (Tseng et al. 1991), organic enrichment (Lemonnier et al. 2017) and nutrient concentrations and their ratios (Boyd 1995, Paerl & Tucker 1995). Diatoms require a wide variety of inorganic nutrients for growth, but the most important are nitrogen and phosphorus (Dawes 1981). The requirement for silica for the growth of diatom shells is mostly derived from shrimp pond sediments (Cremen et al. 2007).

Higher amounts of nutrients and metabolic wastes enter the water as the daily feed allotment increases in response to shrimp biomass increase during the progression of the culture. It has been reported that as much as 80% of the nitrogen from the shrimp feed accumulates in the water as excess (Sanders et al. 1987). Ammonia is formed during protein catabolism in shrimps and can account for 40–90% of nitrogen excretion (Parry 1960). Nitrate is a product of nitrification in pond water and is dependent on the addition of fertilizers and feed. Remineralization of nitrogen from feed and from shrimp excreta might have led to a gradual increase in the availability of nitrate and ammonium-nitrogen (NH_4^+-N) in the ponds up to 36 DoC; however, the concentrations of ammonium recorded during this study (1–11 µM) were within the optimum range for the growth and survival of penaeid shrimps (Chien 1992). Higher concentrations of unionized ammonia (NH_3^-) have been reported to cause stress to cultured shrimps (Burford & Lorenzen 2004); however, the maintenance of optimum pH (7–8) in the ponds helped in regulating the ammonium levels, thereby keeping its unionized form under control. A dramatic decrease in the concentrations of nitrate and ammonium after 36 DoC and an increase in phytoplankton abundance until 96 DoC were observed (Fig. 2). As nitrate and ammonium are essential nutrients that encourage the growth of phytoplankton (Shan & Obbard 2001), the lower levels of these nutrients recorded after 36 DoC were possibly due to their uptake by phytoplankton. Thus, uptake by phytoplankton, as well as adequate aeration and addition of probiotics, may have prevented the build-up of ammonia to toxic levels (Martinez-Cordova et al. 1998, Lorenzen 1999, Fernandes et al. 2010).

Higher concentrations of chl *a* observed towards the end of the production cycle may have been due to the significant increase in phytoplankton abundance, mainly by 2 co-dominant species of the centric diatoms *Thalassiosira* sp., reaching nearly bloom proportions. Such an increase in abundance of plankton over the culture period has been reported previously in shrimp cultures (e.g. Alonso-Rodriguez & Páez-Osuna 2003). Since the bloom was composed of multi-species of *Thalassiosira* sp. as well as pennate diatoms such as *Nitzschia closterium*, *Pleurosigma elongatum* and *Thalassionema nitzschioides* in moderate numbers, similar to observations of Smith (1985), the bloom persisted from the middle to the end of the culture period. *Thalassiosira* spp. is a nanoplanktonic diatom that grows rapidly when nutrients are increased; it has been reported as a major component of the spring diatom bloom in shallow euphotic zones of many coastal waters (Guillard & Kilham 1977, Waite et al. 2005) and also a significant proportion of phytoplankton community in densely stocked shrimp ponds (Melo et al. 2010, Lemonnier et al. 2016). By virtue of their importance in substantially contributing to the growth performance of *L. vannamei* even at adult stages (Moss 1994) and provision of adequate levels of the dietary requirements of PUFAs, eicosapentaenoic acid and/or docosahexaenoic acid and arachidonic acid (Volkman et al. 2006), these centric diatom species are highly desirable in shrimp ponds.

As also reported by Yusoff et al. (2002) and Lemonnier et al. (2017), phytoplankton blooms occur in response to increased amounts of nutrients from the metabolic wastes of shrimp. Smith (1983) suggested that in tropical areas where the temperature is high and light is abundant, phytoplankton blooming could be due to the rapidly changing nutrient concentration and nitrogen:phosphorus ratios. The most favorable nitrogen:phosphorus ratio for blooming diatoms in shrimp ponds has been reported to be 20:1 (Daniels & Boyd 1993). Ratios of nitrogen:phosphorus during 96 DoC varied from 0.3–61, with higher values during 0–36 DoC and then decreasing to <12 with further progression of the culture. Such a decrease in the nitrogen:phosphorus ratio might be related to the accumulation of phosphate towards the end of the production cycle. The build-up of phosphorus might have stimulated the peaking of diatom production (Fig. 2) in the presence of adequate nitrogen towards the end of culture, as has also been observed by Stickney (2005) and Castillo-Soriano et

al. (2013). Interestingly, few studies have reported a dominance of cyanophytes coupled with a high phosphate concentration (Yusoff et al. 2002, Shaari et al. 2011). Silicate:nitrogen ratios affecting diatom dominance has been reported by Sommer (1989). Though silicate was not measured in this study, we assumed from a similar study (Smith 1994) that amorphous silica present in the shrimp pond sediments was adequate enough in promoting diatom growth and apparently depressed the growth of cyanophytes.

With an increase in phosphorus loading, a shift in communities from diatoms to dinoflagellates has been observed by Hodgkiss (2001). In our study, few heterotrophic dinoflagellates belonging to the genera *Dinophysis* and *Protoperidinium* were recorded intermittently during the production cycle. Additionally, the occurrence of UID2 in high abundance ($>10^5$ cells l^{-1}) at 24 DoC was recorded. However, none of these dinoflagellate species belonged to the harmful category. Leaching of humic acids and other organic substances from feed is known to stimulate the growth of dinoflagellates (Prakash & Rashid 1968). The occurrence of *Protoperidinium* spp. is common along the west coast of India (e.g. D'Silva et al. 2011). These non-pigmented, phagotrophic dinoflagellates often occur in high abundance during diatom blooms and are significant consumers of blooming diatoms (Sherr & Sherr 2007). In the present study, the lower abundance of *Thalassiosira* spp. on 24 DoC appears to be related to the grazing activity of UID 2.

Similarly, planktonic ciliates comprising mainly *Dadayiella acuta*, *Tintinnopsis minuta*, *Strombidium caudatum*, *Euplotes* spp. and *Eutintinnus elongatus* recorded in this study are known to be vigorous grazers of phytoplankton (Pierce & Turner 1993, Tillmann 2004). Their lower abundance throughout this culture period, except for the high value of 12 016 cells l^{-1} on 96 DoC, is probably related to the more abundant availability of phytoplankton, which many ciliates are known to feed upon (Liu et al. 2018). Nearly all species of *Strombidium* are suspension feeders, feeding mainly on larger-sized diatoms (Fenchel 1968). A high abundance of *S. caudatum* and phytoplankton towards the end of shrimp culture is reflective of their intense grazing activity. Higher abundance of *Euplotes* spp. on 96 DoC could be related to bacterivory, as they are known preferential grazers of bacteria attached to surfaces (Sieburth 1979), especially those associated with the decomposition of animal and plant tissues (Fenchel 1968). The higher abundance of ciliates at the end of the culture period might be in response to higher inputs of organic matter (Decamp et al. 2007, Melo et al. 2010), rapid reproduction rates and short generation times as well as their ability to use a large spectrum of food resources (Capriulo & Carpenter 1983, Capriulo et al. 2002, Urrutxurtu 2004)

Higher abundances of *Eutreptiella marina* are associated with nutrient enrichment (Urrutxurtu 2004), and the rapid changes in abundances could be due to the grazing impact of ciliates (Epstein et al. 1992). *Eutreptiella* sp. are mixotrophs which feed on eubacteria and *Synechococcus* sp. (Yoo et al. 2018) and employ a range of nutritional modes from osmotrophy to phagotrophy, enabling them to exploit both inorganic and organic resources (Müllner et al. 2001). The growth of *Eutreptiella* sp. far exceeds the grazing pressure by mesozooplankton when nutrients are not limiting, as in the case of shrimp ponds (Olli et al. 1996). In the coastal waters of China, blooms of *Eutreptiella gymnastica* coincided with high phosphate concentrations (Xu et al. 2012). Invertebrate metazoans such as copepod nauplii and copepodites, juvenile ostracods, decapod larvae and polychaetes, which contributed 20% to the microzooplankton abundance in the present study, are also known to be potential grazers of phytoplankton (Berggreen et al. 1988). Since microzooplankton grazing can remove up to 50% of the stocks of small phytoplankton (Zhang et al. 2011) and >90% of dinoflagellate production (Epstein et al. 1992), the preponderance of microzooplankton in our shrimp ponds would have exerted positive control on the phytoplankton bloom and prevented the latter from reaching undesirable proportions. In addition, predation of the microzooplankton by shrimps (Coman et al. 2003) in turn results in the transfer of a significant proportion of the nutrients from natural biota to the shrimp tissue (Anderson et al. 1987). Based on previous studies (Calbet & Landry 2004) and the abundances observed in this study (10^5 ind. l^{-1}), there is little doubt that microzooplankton forms a significant component of the natural biota of shrimp ponds and are a key link between phytoplankton and shrimps.

By virtue of their sensitivity to environmental changes, plankton communities are often considered excellent indicators of water quality (Li et al. 2009). During the culture period, higher abundances of diatoms, dinoflagellates and ciliates coincided with very low species richness and evenness. Lower phytoplankton diversity (<1.6) observed in the shrimp ponds compared to the coastal waters is attributable to chlorination of the seawater for the initial filling, zero-water exchange and dominance of 3 plankton species. In shrimp ponds adjoining Hangzhou Bay, nitrogen and phosphorus load were found to strongly

influence the proliferation of Chlorophyta blooms and low phytoplankton diversity (Ni et al. 2018).

CCA analysis, which was performed to analyze the relationship between phytoplankton and environmental variables and to understand the main driving factors of phytoplankton community structure, suggested that many centric diatoms (*Ceratualina pelagica*, *Cyclotella ocular*, *Dactyliosolen fragilissimus* and *Leptocylindrus minimum*) and pennate diatoms (*Achnanthes frigidus*, *Amphiprora paludosa, Diploneis suborbicularis* and *T. nitzschioides*) were growing under high nitrate and ammonium conditions during the first month of shrimp culture. Since a biosecured zero-water exchange system of shrimp farming was followed in the present study, the increasing temperature led to a concomitant increase in salinity, triggering the bloom of the centric diatom *Thalassiosira* spp. and consequently causing a decrease in DO levels. As 2 species of *Thalassiosira* sp. were the main contributors to the high biomass of phytoplankton at the end of the culture period and were negatively correlated with nitrate and ammonium, it indicates that the phytoplankton biomass was related to the removal of nitrogen. Though nitrogen is an essential element for phytoplankton growth, and almost all chlorophyll-containing algae grow either on nitrate or ammonium (Syrett 1981), diatom growth is particularly promoted by inorganic nitrogen sources (Robert et al. 1986). Besides providing food, shade and increased oxygen levels and preventing the growth of undesirable benthic algae, reduction in toxic ammonia concentrations by diatom blooms have been documented in shrimp ponds (Chien 1992, Burford 1997).

As the shrimp culture and build-up of the algal biomass progressed, excess phosphate derived from the decomposition of shrimp feed favored the bloom of a semi-heterotrophic euglenoid unarmored flagellate, *E. marina* and of a few dinoflagellates. The rapid growth of *E. gymnastica* and dinoflagellates in enriched phosphate conditions was also observed in other studies (Xu et al. 2012, Barcelos e Ramos et al. 2017). Increased turbidity due to higher suspended matter in shrimp ponds may stimulate picoplankton abundance, which can even dominate the phytoplankton community (Burford 1997, Lucas et al. 2010); however, this aspect was not addressed in the present study but will definitely be considered in future investigations.

Low diversity of plankton communities and the dominance of particular species indicates that the shrimp ponds in our study had the tendency to become hypernutrified. However, this study has shown that the effective uptake of nutrients through increased abundance of desirable diatoms and their control by microzooplankton with the progression of the culture helped to maintain the water quality and consequently contributed to good shrimp yield. Many studies have indicated that mixtures of diatoms and flagellates have produced good results in terms of shrimp growth and survival (Gaxiola et al. 2010). In addition, at harvest the undesirable environmental impact due to the discharge of pond water into the coastal waters would be significantly lower.

Acknowledgements. The authors are thankful to the Director, CSIR-National Institute of Oceanography, Goa (India), for encouragement and facilities. Financial support for this study came from project No. PSC0206 of CSIR-NIO (India). The authors are also thankful to the 4 anonymous reviewers for their valuable suggestions in improving the manuscript. This represents Contribution No. 6466 of the CSIR-National Institute of Oceanography, Goa India.

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Editorial responsibility: Louis Lebel, Chiang Mai, Thailand

Submitted: March 29, 2019; Accepted: October 21, 2019
Proofs received from author(s): November 25, 2019